Journal of Research on the Lepidoptera 24(2): 154-175, 1985

Notes on *Caligo memnon* Felder and *Caligo atreus* Kollar (Lepidoptera: Nymphalidae: Brassolinae) in Costa Rica and El Salvador

Allen M. Young

and

Alberto Muyshondt

Invertebrate Zoology Section, Milwaukee Public Museum, Milwaukee, Wisconsin 53233
and
Lomas Verdes, San Salvador, El Salvador, C.A.

Abstract. The life cycles and associated natural history for *Caligo memnon* Felder and *Caligo atreus* Kollar (Nymphalidae: Brassolinae) were studied in Costa Rica and El Salvador (the latter for *C. memnon* only). Brief, general descriptions of early stages are given as supplementary data to previously-published information on early stages, especially for *C. memnon* and much less so for the more elusive *C. atreus*. Preliminary field data on the relative abundance of both species at banana baits at one Costa Rican locality are also summarized. Both species display a variety of traits compatible with their life style of dwelling close to the ground in tropical forest habitats, including cryptic color patterns and behavior in both adults and caterpillars, and the feeding by adults on fallen fruits. *Caligo* females may have to mate more than once to fertilize all of their eggs, and males are attracted to electric lights. Major caterpillar food plant families in Central America are Musaceae and Maranthaceae, and our data suggests some divergence in food plants between these two species.

Introduction

". . .the great *Caligo*, with the owls' eyes on the under side of its wings, makes for the banana. . ."

from: K. Guenther, 1927, *A Naturalist in Brazil,* London: G. Allen Ltd.

K. Guenther's remark constitutes one of the best known biological attributes of many brassolids, morphids, and satyrids in the American tropics, namely, the feeding association of the adult butterflies with fallen, rotten fruits such as bananas. Our paper calls attention to some life cycle and natural history features for the butterflies *Caligo memnon*

Felder and *Caligo atreus* Kollar (Lepidoptera: Nymphalidae: Brassolidae) as studied in Costa Rica (both species) and El Salvador (*C. memnon* only). We add to the observation and studies of *Caligo* biology already conducted in Central and South America by a variety of workers (e.g., Boudar, 1915; Davis, 1915; Bodkin, 1916; d'Almeida, 1922; De Azevedo, 1923; Waterston, 1923; H. Fruhstorfer in Seitz, 1924; Clease, 1926; Hoffman 1933; Breyer, 1929; Bullock, 1959; Labrador, 1961; Malo, 1961; Malo and Willis, 1961; Harrison, 1963; Tournier et al., 1966; Condie, 1976; Casagrande, 1979a, b, c, d; DeVries, 1983). Our paper provides a first description of larval food plant and early stages for *C. atreus* as well as new behavioral data for *C. memnon*, a widespread Central American species (Seitz, 1924) well known for its occasional economic impact as a defoliator of bananas (*Musa* sp., Musaceae) (Harrison, 1963). The early stages of both species have also been described by Condie (1976).

Materials and Methods

In Costa Rica, larval *C. atreus* Koll. was studied at "Bajo la Hondura," a rugged montane rain forest site near Coronado (9°03'N, 83°39'W), San Jose Province, during June-August 1973. The complete life cycle of *C. memnon* in Costa Rica was studied at the "Barranca Site," a tract of semi-deciduous lowland tropical forest near Puntarenas (9°58'N, 84°50'W), Puntarenas Province, during August-September 1973). In addition, adult behavior in both species was studied at "Cuesta Angel," a montane rain forest site (about 1100 m elev.) near Cariblanco (10°16'N, 84°10'W), Heredia Province, and at "Finca La Tigra," a premontane tropical rain forest site (about 220 m elev.) near La Virgen (10°23'N, 84°07'W), Heredia Province. Both sites were visited intermittently for one to five days between 1974 and 1983 for the purpose of observing sex ratios of butterflies at rotting banana fruit bait placed in one or more piles on the ground at the edge of primary or mixed advanced secondary-primary growth rain forest.

Adults of these species are easy to distinguish in the field by their very distinctive wing-color patterns, both dorsally and ventrally (Fig. 1). Life cycle studies of *C. memnon* in Costa Rica were limited to the Barranca Site (Fig. 2), even though this species, and a closely related one, *C. eurilochus* Cramer, are widespread throughout the country. And although *C. atreus* is also common in Costa Rica, observations on the larval stage and pupation were limited to material discovered at the rugged, often mist-shrouded Bajo la Hondura site (Fig. 3). The Costa Rican field work was confined to one of us (A.M.Y.) while the other of us (A.M.) studied *C. memnon* at various localities in the San Salvador area of El Salvador over several years, and with assistance from other members of his family. *Caligo* is generally rare in El Salvador, and observations on *C. memnon* there were limited largely to culturing adults in an enclosed courtyard in Lomas Verdes. Observations were made, however, on the general occurrence of *C. memnon* in the country, and associated habitats. Adult feeding behavior relative to that of other brassolids was also studied. These observations included surveying the abundance of adults of both species at two piles of rotting bananas (approx. 40 bananas per pile) placed in the same two forest-floor sites at "Finca La Tigra" over several years. These baits

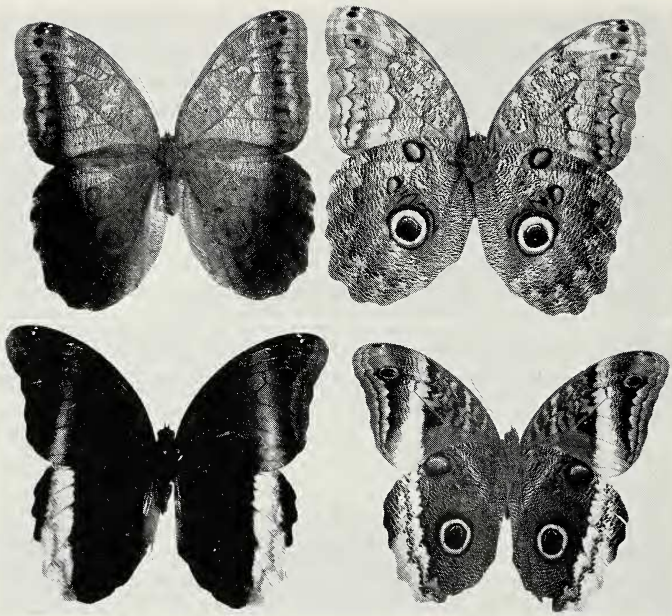

Fig. 1. Adult *Caligo memnon* above, dorsal and ventral aspects; *Caligo atreus* below. From Costa Rica.

were visited several times of the day beginning on the day after they were set out.

In doing so, it was possible to obtain data on the relative number of butterfly "sightings" on a given date for both species.

In the Costa Rican studies, eggs and/or larvae were confined to large clear plastic bags containing fresh cuttings of the food plants. The bags were kept tightly closed and notes were taken on the appearance and behavior of individual life stages. Such observations complemented field observations of larvae on food plants in the wild. We generally followed the same methodology used to conduct similar studies on other brassolids, such as *Opsiphanes* (see Young and Muyshondt, 1975).

Results

Larval Food Plants. In El Salvador, *C. memnon* uses several Musaceae as larval food plants: *Musa* spp., at the Barranca Site, *H. latispatha*. The larval food plants of *C. memnon* in both countries completely overlap those of *Opsiphanes tamarindi sikyon* Fruhstorfer (Young and Muyshondt, 1975). In both countries, *C. memnon* is found from sea level to about 1300 m elev., although the butterfly is far more abundant locally in Costa Rica. It shares with *C. atreus* and *C. eurilochus* the habit of thriving in shaded forest habitats, which, in most of El Salvador, are quite scarce. In Costa Rica, many Musaceae, particularly *Heliconia* species, are widespread and abundant in forest habitats at various elevations (see Daniels and Stiles, 1979). *Caligo* probably exploits various Maranthaceae as larval food plants,

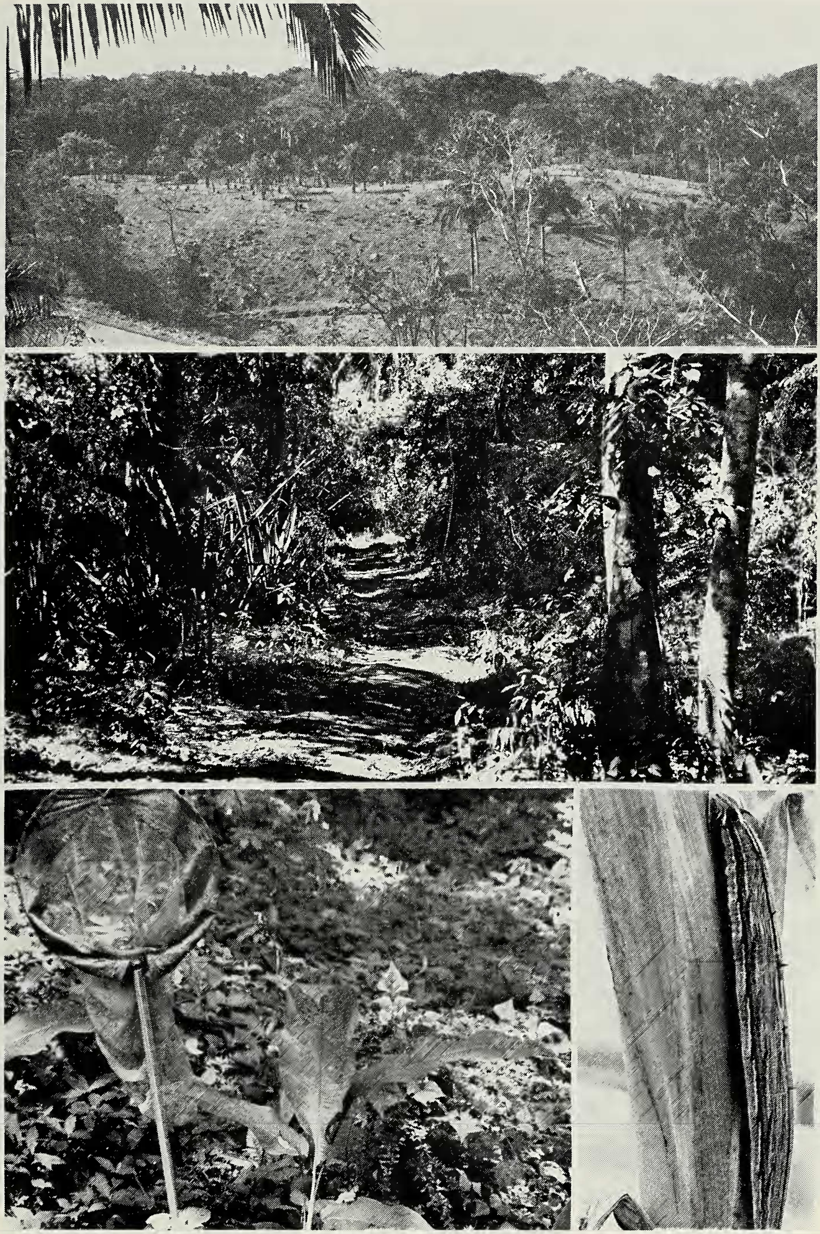

Fig. 2. Barranca Site locality in northwestern Costa Rica where *C. memnon* life cycle was studied. From top to bottom: overview of locality, forest habitat, and *Heliconia latispatha* larval food plant.

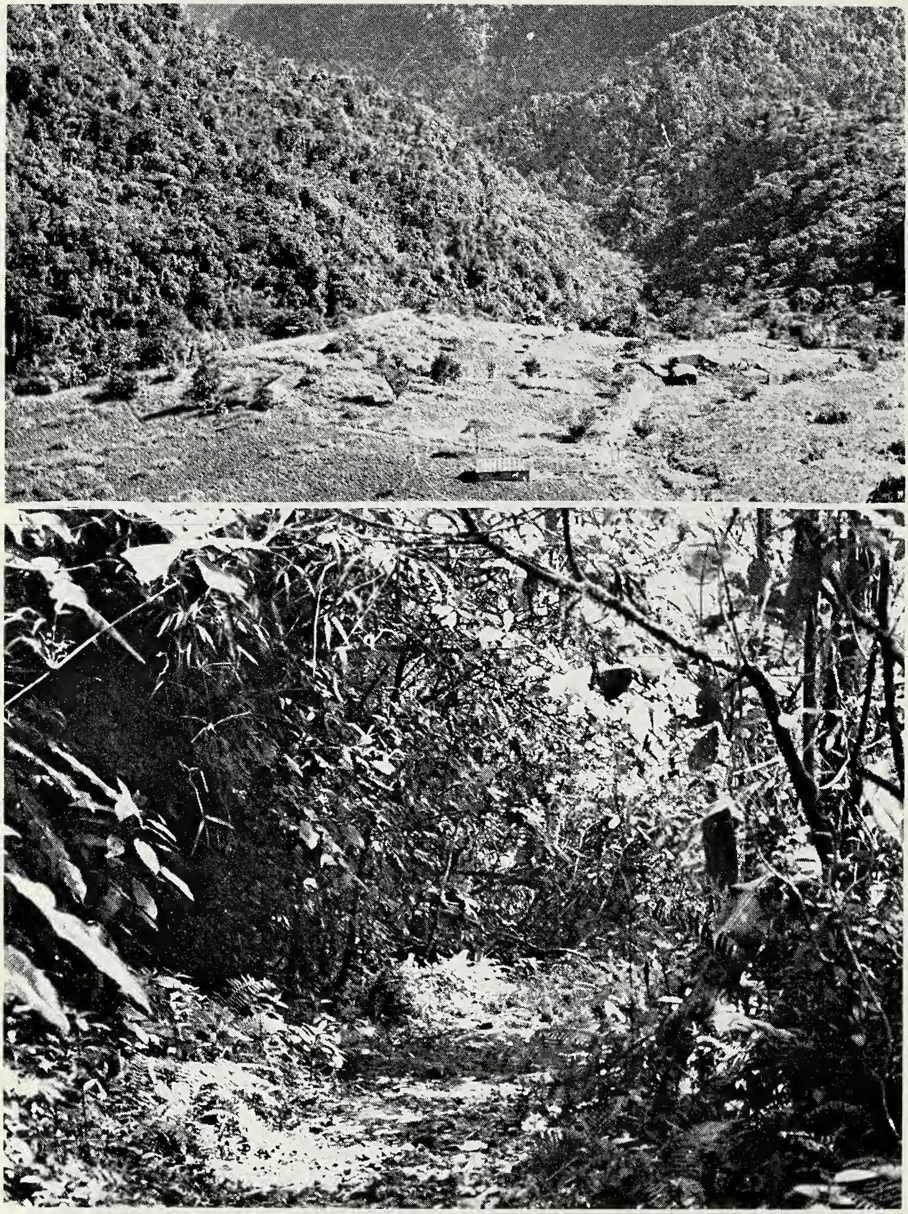

Fig. 3. Bajo la Hondura locality in Costa Rica where *C. atreus* caterpillars were discovered. Top: overview of rain forest ravine where this butterfly thrives, and below: foot trail in forest where *C. atreus* caterpillars were found on well-shaded *Heliconia* sp. plants.

particularly in Costa Rica where more forest is available, as these are known food plants for South American species (Casagrande, 1979a and associated references on early studies in South America). H. Fruhstorfer in Seitz (1924) suggests that larvae of many species feed interchangeably on Musaceae and Maranthaceae, closely allied taxa within the Zingiberales (Cronquist, 1968). Condie (1976) reared *C. memnon* on both *Heliconia* and *Canna* (Cannaceae) and *C. atreus* on *Calathea* (Maranthaceae) in Costa Rica, after discovering eggs on these plants in the field. The apparently wide regional distribution of individual species of *Heliconia* in Costa Rica, such as *H. latispatha* which is abundant in forests on both the Atlantic and Pacific slopes of the Central Cordillera from sea level to about 1600 meters elevation (Standley, 1937) as well as being widespread throughout much of Central America and northern South America, accounts for the widespread distribution of *Caligo* and other Brassolidae.

At Bajo la Hondura, *C. atreus* larvae were discovered on an unidentified species of *Heliconia* growing along a forest trail. There was a clump of four plants with leaves up to about three meters high and in the dense shade to one side of the trail (Fig. 3).

We have not found *Caligo* on any palmaceous plants in Costa Rica and El Salvador, even though such plants are sometimes exploited by the larvae of other Brassolidae (see Young, 1977, 1983; Young and Muyshondt, 1975). We suspect that *C. memnon* and *C. atreus* in Costa Rica may overlap considerably in the *Heliconia* species exploited as larval food plants (see also Condie, 1976), since both butterfly species are sympatric over a wide elevation. Although *C. memnon* and the very closely related *C. eurilochus* are well known defoliators of banana plants in commercial plantations in Central and South America (e.g., Boudar, 1915; De Azevedo, 1923; Malo, 1961; Malo and Willis, 1961; Harrison, 1963; Tournier et al., 1966), *C. atreus* is not generally considered as a pest species. The introduction into Costa Rica and other parts of Central America of commercial banana species from the Old World tropics in the late 1800s, such as *Musa paradisiaca* ("platano") and *M. sapientium* (Standley, 1937), may have led to a shift in larval food plants for some *Caligo* species (such as *C. memnon*) associated with *Heliconia* and Maranthaceae, and not others (such as *C. atreus*).

Early Stages. Harrison (1963) and Casagrande (1979a, b, c, d) give detailed descriptions of the early stages for *Caligo beltrao* Illiger and *C. memnon*. Because the early stages of *C. beltrao* probably typify those of most *Caligo*, the details for *C. memnon* are not given here. For *C. atreus* we have only partial data, namely, for fifth-instar larva and pupa only. We therefore emphasize the final instar larva and pupa of *C. atreus* relative to those of *C. memnon*, for which information is available (e.g., Harrison, 1963).

Harrison (1963) describes, without figures, all stages of *C. memnon*. We therefore have included illustrations of eggs and first three instars of larvae for this species (Fig. 4), eggs, first, from the Barranca Site in Costa Rica, the fifth-instar larva (Fig. 5), and prepupa and pupa (Fig. 6). The following details of the early stages were not reported by Harrison.

The cream-colored spherical and vertically-ribbed egg (about 1.7 mm dia.) turns reddish within a day of hatching, then darkens a few hours prior to hatching. While still cream-colored, a very thin brown line forms almost equatorially on the egg. Body color of the third-instar larva dull light green, the dorsal and medial oval spots (Fig. 4) ringed with black and lavendar in the middle, with white posteriad. The anterior of oval spot has a tuft of black setae (on the sixth segment) and a second, much smaller tuft at end of the seventh segment. End of eighth segment with tiny dorsal spot of red. First thoracic segment mottled in white and brown, second one with small dorsal, medial patch of red with a white spot inside of it. Third thoracic segment devoid of conspicuous markings. Head capsule banded with stripes of tan and dark brown. Both head capsule and body covered, particularly laterally, with fine covering of very short white setae. Long white setae adorn four protuberances from the dorsal and lateral areas of the head capsule (Fig. 4).

Body ground color in fifth-instar larva (Fig. 5) light brown; conspicuous dorsal medial stripe dark brown. Dorsal oval patch on third abdominal segment orange with a thin brown line in center that does not reah posterior end of patch. Anteriorly this line fuses with a tuft of dark brown setae at edge of second abdominal segment. Posterior edge of fourth abdominal segment with very small orange spot with a tiny tuft of setae. A similar tuft appears at posterior edge of fifth abdominal segment. Various angular lines and markings of grainy brown spots radiate out from medial longitudinal body stripe. On thoracic segments stripe thickens and fills with shades of light tan. The tail forks of fifth-instar larva of *C. memnon* are about 10 mm long and covered generously with long light-tan setae (Fig. 5). A whitish-yellow line runs lengthwise through spiracular region and spiracles are ringed in reddish-brown. Ventrally body is dark purple and covered with many small setae giving it a brownish sheen.

The head capsule of the fifth instar striped similarly to that of previous instars and arrangement and sizes of the four prominent tubercles immediately separates this species from *C. atreus*. The dorsal-most pair of tubercles are longest, being about four mm long and with many long white setae at tips; lower half of these tubercles dark brown. The remaining three pairs progressively shorter but similarly colored and covered with setae. Length of these remaining pairs of tubercles (there are a total of four pairs) decreases as follows: subdorsal set: 2 mm long, lateral set: 1 mm long, and sub-lateral set: 0.5 mm long. Mandibles light brown. Ventrally eversible "neck" gland found just anterior to first pair of legs; gland is reddish, and present in all instars. It is similar to the same gland found in *Morpho* larvae (Morphidae).

Pupa (Fig. 6) warrants more detailed description than given in Harrison (1963). Pupa, 43 mm long by 21 mm wide (dorsal-ventral axis, through wing pads), mottled in various shades of brown and strongly angular on either side of thorax (Fig. 6). Cremaster beige, with faint brown line immediately ventral to the orange spiracle markings. Abdominal area with faint oblique stripe pattern of alternating shades of browns and yellows, but effect is not nearly as pronounced as in *C. atreus*. Wing pads resemble dried, dead leaves in appearance, but each forewing case bears triangular and convex silver spot along trailing edge, and second but tiny one immediately adjacent to larger spot (Fig. 6). Silver spots on wing pads in *C. memnon* pupae are not so pronounced as those found on *C. atreus* pupae. A conspicuous feature that immediately separates pupae of *C. memnon* from those of *C. atreus* is presence of distinct groups of stout bristles seen in former species and not in latter: All of these bristles originate from the ventral medial area of abdomen, and they are distributed as follows (Fig. 6): Abdominal segment 1: 10 bristles, central and scattered; segment 2: six bristles, central and scattered; segment 3: four

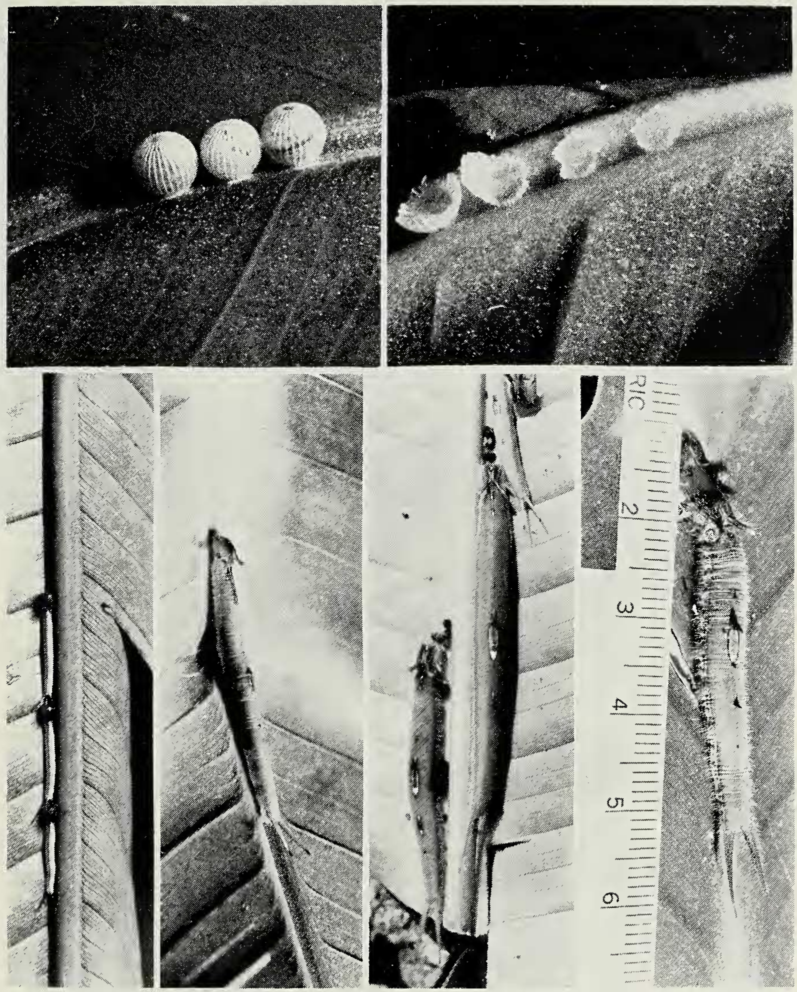

Fig. 4. Early stages of *C. memnon* from Costa Rican studies. Clockwise, from upper left corner: triplet of eggs showing characteristic rings, partly-devoured egg shells, third, second, and first-instar caterpillars in typical resting positions on ventral sides of leaves of *Heliconia* sp. plants. Note group behavior of first-instar caterpillars (lower left).

bristles, central ad scattered; segment 5: two rows of many bristles; segment 6: two rows of approximately 50 bristles; segment 7: small, tight central cluster of less than 10 bristles. These bristles erect and black, and do not appear to have discernible tactile function. On dorsal area of head two additional clusters of bristles on each side; each cluster consists of two rows of approximately 25 bristles in all. These rows extend over area of the compound eyes and down underneath them. In

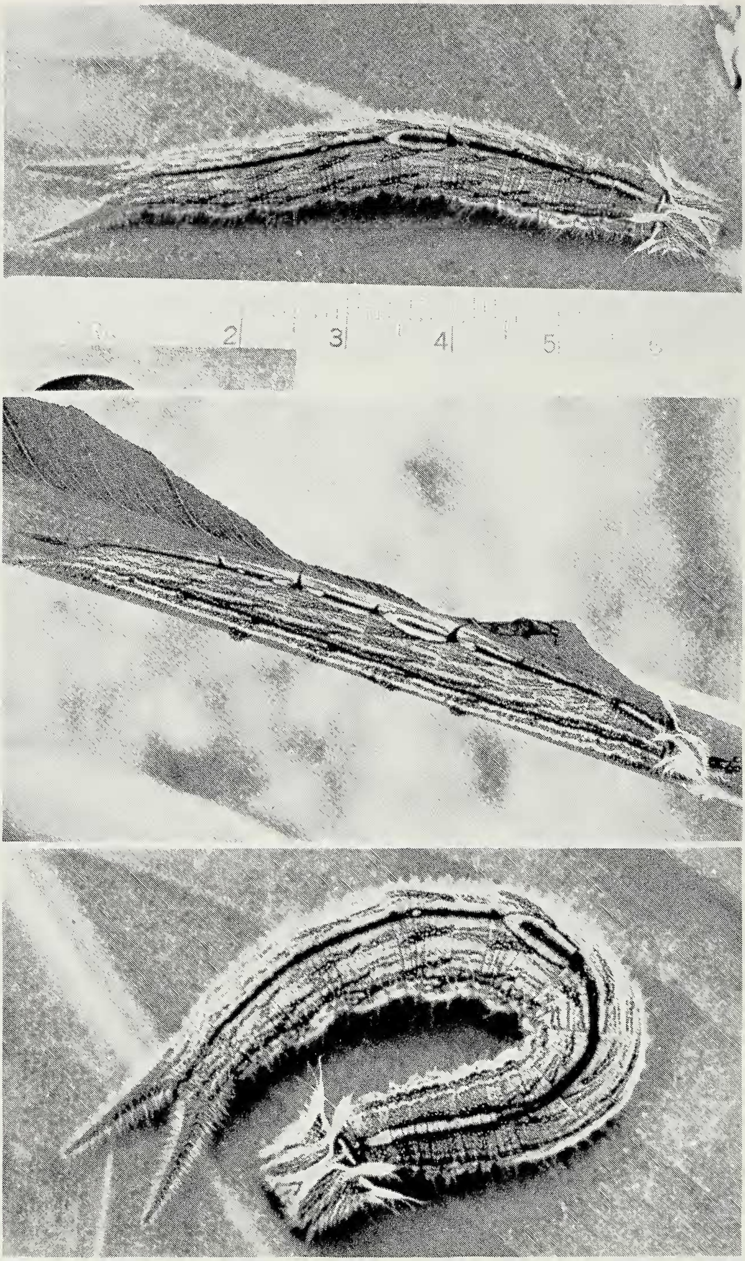

Fig. 5. Fifth-instar caterpillar of *C. memnon*: dorsal (top), lateral (middle) and head capsule (below) aspects.

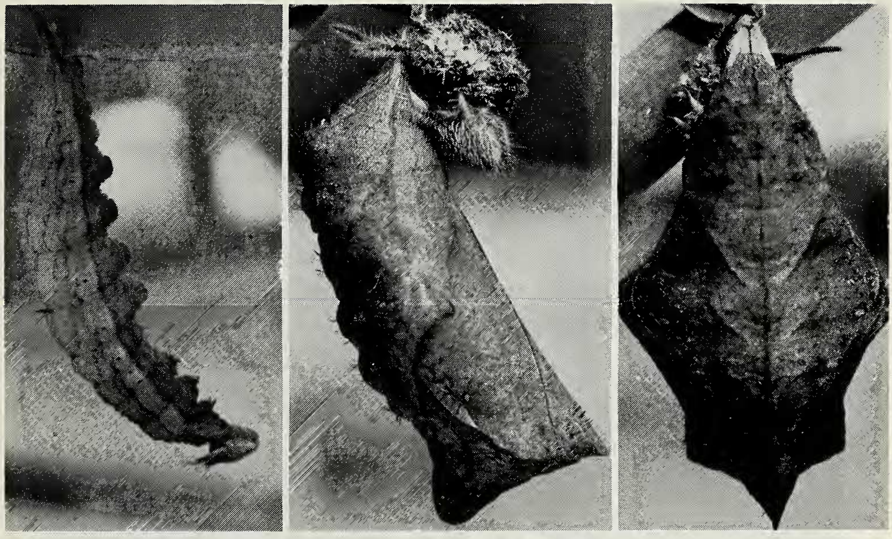

Fig. 6. Pupa (chrysalis) of *C. memnon* and pupation behavior: from left to right: prepupa, pupa-lateral aspect, and pupa-dorsal aspect. Note positions of groups of stout bristles clearly visible in the lateral view of the pupa. These bristles are absent in *C. atreus*.

central area of head dorsally another row of bristles, and a few of these extend ventrally.

Pupa results from molting of a prepupa that remains motionless for at least one day prior to molt (Fig. 6). When prepupa is deliberately disturbed, it everts ventral neck gland very quickly, although no noticeable odor detectable. Prepupa (Fig. 6) is light greenish-brown with a yellow hue. Although Harrison (1963) reports a pupal stage of 11-14 days, in our studies the pupa of *C. memnon* lasted 20 days under varying temperature and humidity conditions associated with rearing in Costa Rica. We reared a total of eight larvae, and without mortality. *Caligo* species are generally hardy enough for mass laboratory rearing associated with other kinds of research studies (e.g., Wasserthal and Wasserthal, 1980).

Fifth-instar larva of *C. atreus* generally much darker in overall body coloration (Fig. 7) allowing it to blend with shaded and subdued hues of petioles of *Heliconia* fronds on which they rest during daylight hours. The initial discovery of two *C. atreus* larvae, one on each of two different *Heliconia* plants about 20 meters apart, was greatly facilitated by the noticing of the ornate head capsules in patches of sunlight in the otherwise dark surroundings. The discovery was made at about 1400 hours on 26 June 1973 at Bajo la Hondura at a time when prevailing weather conditions were unusually sunny.

Fifth-instar larva of *C. atreus* measures 113 mm long by 12 mm at thickest (mid-section) region of body at time it stops eating in preparation for pupation. Tall "forks" are eight mm long and head capsule width is 6.5 m. There are five sets of tufts of long setae distributed lengthwise along dorsal medial line of body in following manner: Abdominal segment 3: 4 mm long; segment 4: 0.5 mm long; segment 5:

Fig. 7. Fifth-instar caterpillar of *C. atreus* on *Heliconia* at Bajo la Hondura. Shown are typical resting positions of the cryptically-colored caterpillars on the well-shaded stems of the larval food plant; caterpillars almost concealed save for light highlighting the head capsules.

5.5 mm long; segment 6: 6.2 mm long, segment 7: 1 mm long. Dorsal-most protuberances of head capsule (Fig. 8) exhibit a strong "right-angle" bend or curvature, with apical half facing outward to one side of head capsule. Apical portion of each of these dorsal protuberances appears "swollen" in size relative to stem portion, and bears many long, filamentous white setae (Fig. 8). Remaining pairs of tubercles much smaller, straight in appearance and bear setae. Head capsule is basically tan with several dark brown vertical stripes, and posterior edge chocolate brown, a color extending into posterior sides of the large dorsal protuberances. Frontally all tubercles tan, although stem areas of most dorsal ones reddish-brown. Chocolate-brown coloration of posterior region of dorsal-most tubercles extends straight down side of head capsule as a thick brown stripe. Frontal plates of head capsule streaked vertically with thin lines of dark brown on otherwise tan or beige background color.

Above spiracles body mottled olive green hue with irregular blotches of dark brown. Three thoracic segments green with distinct dorsal-medial grayish-tan line. Dark brown "mottling" on remaining body segments (Fig. 8) forms series of inverted "W" patterns most evident looking down on larva directly from above. Apex of several of these "W" markings with tufts of compacted setae. These markings most prominent on abdominal segments four and five, and become faint near either end of body. Thin line of red faintly bordered in white and white speckling runs through spiracle region on either side of body. Ventrally body cuticle and prolegs red. Sparse covering of short orange setae blankets most of body dorsally. Thoracic spiracles thickly ringed in brown which extends out posteriorly from each, disrupting the thin white line runing lengthwise through spiracle region (see above). Anteriorly-deflected tufts of long, compacted setae orange-brown near the base and black at tips. Eversible gland located ventrally just anterior to first pair of true legs pinkish and not red as in *C. memnon.*

Stout pupa (Fig. 9) 48 mm long by 20 mm (side to side, through the thoracic area), and patterned in shades of brown and deep yellow. Dorsal-ventral thickness through thorax is about 14 mm, and about 13 mm through abdomen. Oblique stripe pattern of dark brown lines on a yellowish background color most evident in abdominal region (Fig. 9), and silvery spots on wing pads far more prominent and convex in this species as compared with *C. memnon* (Fig. 9). Noticeably absent are several sets of rigid black bristles noted for pupa of *C. memnon.* Initially silvery, spot pattern on wing pads becomes golden within five days following pupation. Within a day of eclosion, pupa darkens noticeably, beginning in wing pads (Fig. 9), and eclosion is rapid, being completed within five minutes (Fig. 9). Terminal five segments of abdominal region capable of rapid, often violent, movements, and move freely from rest of pupa upon disturbance. "Cleft" noticeable between fourth and fifth abdominal segments where this articulation occurs; it is not noticeable in *C. memnon.* Duration of the pupa was 21 days.

Behavior of Caterpillars. Various authors (e.g., H. Fruhstorfer in Seitz, 1924; Harrison, 1963; Casagrande, 1979a) have described the nocturnal and crepuscular feeding habits of *Caligo* caterpillars, and the ability of caterpillars to spin silken resting mats and pathways to and from feeding sites on the food plants. We confirm these patterns of behavior within *C. memnon* and *C. atreus.* The caterpillars of both species anchor themselves, in all instars, in silken mats on the ventral, dorsal sides of leaves, as well as on the petioles of leaves. We interpret this behavior as part of crypsis, allowing the caterpillar to anchor itself securely at those times of the day and night when it is not feeding. Younger instars generally rest on the leaves proper, and the aggregative behavior of early instars in *C. memnon* (see Fig. 4) is well known (Harrison, 1963). Casagrande (1979a) describes in some detail the gregarious resting behavior in *C. beltrao* caterpillars in various instars. She also noted that when disturbed, caterpillars as a group will wave the head and anterior body segments back and forth. We have observed similar movements in *C. memnon* and *C. atreus,* and caterpillars evert the gland located in the "neck" region at such times. Harrison (1963) noted that sometimes as many as 12 young caterpillars of *C. memnon* comprise a group, and that group size generally diminishes as caterpillars get larger in size. During the fifth instar, for example, usually the caterpillar occurs singly on the food plant, or in groups of two or three (Harrison, 1963). In our studies, we have noticed that first-instar *C. memnon* rest head-to-head along the midrib on the ventral surface of a *Heliconia* leaf. First-instars build silken trails to the edge of the same leaf and feed there in group fashion. Later instars, such as the second and third-instars, exhibit similar resting and feeding behavior on the leaves. When we lay on the ground on our backs and look up through a *Heliconia* leaf having one or more caterpillars on the ventral surface, the insects are practically indistinguishable from the general color of the leaf. But when we turn the same leaf over and look down at the caterpillars, they are very obvious. We suspect, therefore, that the caterpillars of *Caligo* have evolved a form of crypsis most

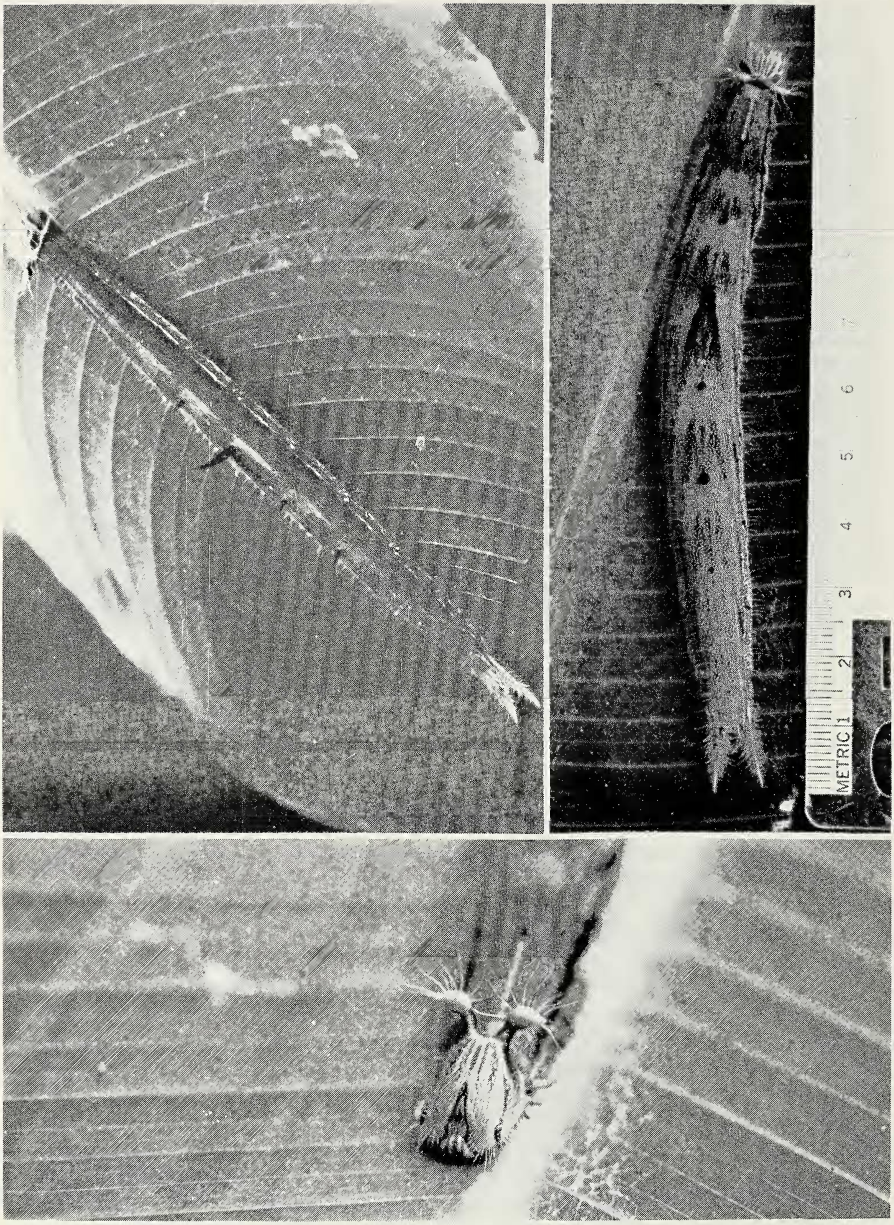

Fig. 8. Fifth-instar caterpillar of *C. atreus*, emphasizing dorsal (upper two photos) and head capsule (below) details.

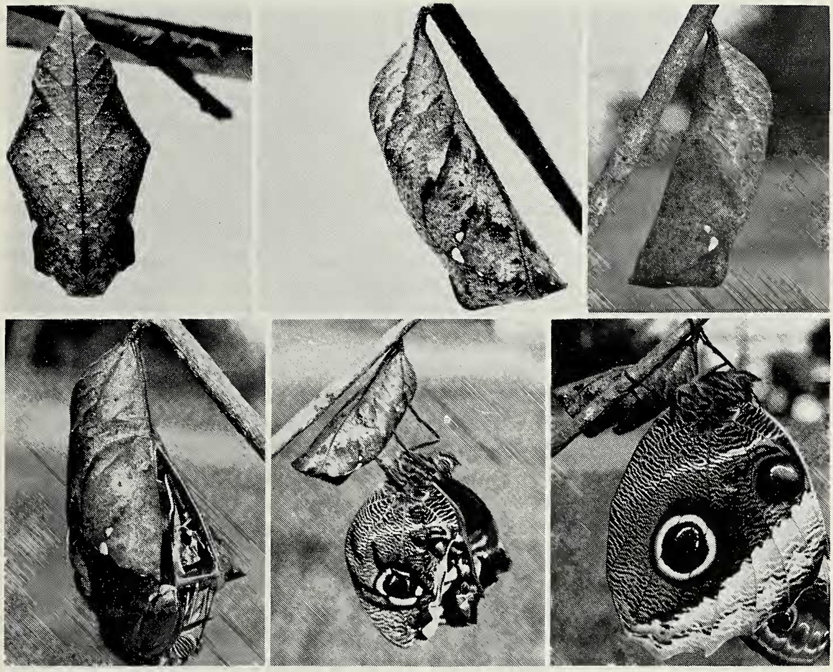

Fig. 9. Pupa (chrysalis) of *C. atreus*, and adult emergence. Note conspicuous silvery-gold spots on wing cases and banding color pattern of abdomen.

applicable to ground-foraging insectivorous and omnivorous predators, ones that look up to the undersides of leaves for their prey.

The more brownish hues of the fifth-instar are adaptations for being cryptic on the similarly colored petioles and trunk areas of *Heliconia* plants in shaded forest habitats, as the caterpillars move to such resting places when they are larger in size. Occasionally, at Cuesta Angel in Costa Rica, one of us (A.M.Y.) has even seen *Caligo* fifth-instars resting on non-food plants adjacent to *Heliconia* plants during the daylight hours.

We have noticed that first-instar caterpillars often rest near vacated egg shells soon after hatching, and that they devour egg shells to varying degrees (see Fig. 4). Egg shells are often only partly eaten.

Hymenopterous parasites are reported in the literature to take heavy tolls on the eggs of *Caligo* species in the wild (e.g., Waterston, 1923; Malo, 1961; Malo and Willis, 1961), including *C. memnon* in Costa Rica (Harrison, 1963). We have not found high levels of such egg parasitism in our studies. In El Salvador, the caterpillars of *C. memnon* are quite susceptible to parasitism by tachinids and we found only one instance of a braconid wasp larva in a caterpillar of this species. Harrison (1963) reports dipterous parasitism on the pupa of *C. memnon* in Costa Rica. Condie (1976) discovered that eggs of *C. memnon* are attacked by *Oencyrtes* sp. (Hymenoptera: Encrytidae) and larvae by *Winthemia pinguis* (F.) (Diptera:

Tachinidae) in Costa Rica.

In our experience, *Caligo* shares with *Eryphanis* (Brassolidae) and *Morpho* (Morphidae) the behavioral characteristic of resting on the trunk of the larval food plant during the fifth-instar period, a time when the appearance of the caterpillar in all three genera changes dramatically to a mottled brown general color (see also Young and Muyshondt, 1973). The caterpillars of these genera also share in common the presence of the eversible ventral gland in the "neck" region behind the head capsule. This structure is absent in the brassolid genus *Opsiphanes* (Young and Muyshondt, 1975) as well as "suspect" satyrid genera such as *Tisiphone (Manataria)*. In *Morpho* the gland, when everted, produces a noticeable rancid margarine-like odor, but such an odor has not been noticed in *Caligo*. The gland is also absent in *Narope ayllastros testaceae* Godman & Salvin (Brassolidae). Whether or not such a gland is defensive in function, or serves to coordinate group behavior in earlier instars, remains to be studied. The strongly nocturnal or crepuscular feeding habits of various larval instars in *C. memnon*, and presumably in *C. atreus*, suggests that the caterpillars are subject to attack by visually-hunting diurnally-active predators.

Behavior of Adults. Various reports, and the present study, indicate that adult *Caligo* butterflies are very crepuscular in their flight activities (e.g., Seitz, 1924; Young, 1972). By observing butterflies on rotting fruit baits (primarily bananas) distributed in piles on the ground cover of premontane rain forest ("Finca La Tigra") and montane rain forest (Cuesta Angel) over several years, the sex ratio of butterflies on such baits is heavily skewed towards males for both *C. memnon* and *C. atreus*. During hot, dry days, such as during the period January-March at such localities, densities of *Caligo* adults at fruit baits increase two or three-fold, a phenomenon we suspect is related to greater moisture stress on these insects. Densities are lowest, in the Costa Rica studies, at the height of the rainy season (July-August). We have no explanations for the apparent temporal changes in abundance of both species at baits in the same forest habitat over the year (Table 1). Other researchers, however, have noted marked cycles of abundance in the Brassolidae in South America (Brown, 1972). The Costa Rican studies (see also Young, 1972) indicate that *Caligo* adults feed on a broad range of rotting fruits, including pineapple, mango and banana. On rainy, overcast days, it is not uncommon to find *C. memnon* adults in particular at fruit baits on forest floors in Costa Rica; otherwise, the daily feeding patterns are very crepuscular, and there is a strong early morning peak of feeding between 0630 and 0800 hours on sunny days. At the Barranca Site, densities of *C. memnon* are very high during the first half of the long dry season of this region, and between 5-20 individuals of this species can be found on a single pile of bait (about 30 cm diameter) between 0700 and 1000 hours. During the latter half of the dry season, densities decline markedly, presumably the result of increased adult mortality and lack of adult recruitment during this period (see Young and Thomason, 1974, for discussion of a similar pattern of dry season population decline in *Morpho peleides* Kollar at this locality).

Interesting to us is the almost exclusive association of *Caligo* adults with fallen fruits as food sources, in contrast with other fruit-feeding Neotropical butterflies. In El Salvador, for example, *Opsiphanes cassina fabricii, Archaeoprepona demophron* Fruhstorfer, *Historus odius* Fabricius, *Smyrna blomfildia* Fruhstorfer, *Colobura dirce* Linnaeus, and others feed on fruits still on trees. The feeding by these adult butterflies occurs shortly after the hanging fruits are pierced and wounded by the scarabeid beetle *Cotinis mutabilis*: the butterflies feed at the fleshy entrance hole made by the beetles as the latter feed inside the fruit. When the beetles exit later, the butterflies fly off and return shortly thereafter. This arboreal fruit-feeding behavior in these nymphalids and brassolids has been noted for various species of *Citrus* as well as breadfruit, *Artocarpus communis*, introduced into El Salvador from the Pacific Islands. *Caligo, Eryphanis, Narope,* and *Manataria*, however, exhibit only ground-level feeding on fallen fruit. Furthermore, we note that most Brassolidae perch lower down in the vegetation than do most Nymphalidae; the highest perching forms include *Smyrna, Colobura, Anaea* and *Prepona*; "intermediate" level perching forms include *Opsiphanes*; the lowest perching forms are those genera mentioned above as well as satyrids such as *Taygetis* sp. While the Brassolidae perch primarily on the trunks of trees, most Morphidae and Satyridae perch on leaves.

Two female *C. memnon* confined to a small courtyard with banana trees produced a total of 165 eggs, with one female living in this outdoor cage for three weeks, and the other one for 18 days. The eggs were discovered as clusters of three to eight eggs, each cluster arranged as an irregular line on the borders or undersides of leaves; no eggs were found on other parts of the banana trees. Adults fed adequately on rotten bananas. The last 30-40 eggs produced jointly by one of the butterflies proved to be infertile, suggesting that female *C. memnon* may need to copulate more than once to fertilize all of the eggs produced in her reproductive life span. Although there was an abundance of banana and *Heliconia* plants in a nearby ravine less than 50 meters away from the courtyard, no male *C. memnon* were attracted into the area. Yet male *C. memnon* were commonly seen at electric street lights in this area at night. Perhaps courtship requires visual contact between the sexes, even though the abdominal scent organs of male *Caligo* are well known (Figs. 10-11). The courtship scent system of *Caligo* has been considered as an evolutionary link of this genus with "suspect satyrids" such as *Bia* and *Manataria*, which have similar structures (Richard I. Vane-Wright, pers. comm.). The arrangement and functioning of the glandular plates of male *Caligo* (Fig. 10) and associated wing hairs (Fig. 11) have been discussed elsewhere (Barth, 1954; Casagrande, 1979d).

In the Costa Rican field studies, one of us (A.M.Y.) also found triplets of eggs placed on new leaf tips of *Heliconia* plants at the Barranca Site. One doublet of eggs was also found on the thick stem about 11 cm off the ground on a very small *Heliconia* plant. Triplets of *Caligo* eggs have also been found along the midrib on the dorsal surfaces of *Heliconia* leaves. In one oviposition act observed, a very tattered *C. memnon* was observed (29 June 1972) at 1745 hours in a light drizzle placing two eggs on the ventral side of the frayed tip of a *Heliconia* leaf. The actual egg-placement behavior lasted several minutes.

Discussion

Our studies of two species of *Caligo* in Central America reveal little difference in their basic natural history. In Costa Rica, both species, *C. memnon* and *C. atreus*, are sympatric throughout the country, particularly in the lowland and premontane tropical wet forest sites associated with the

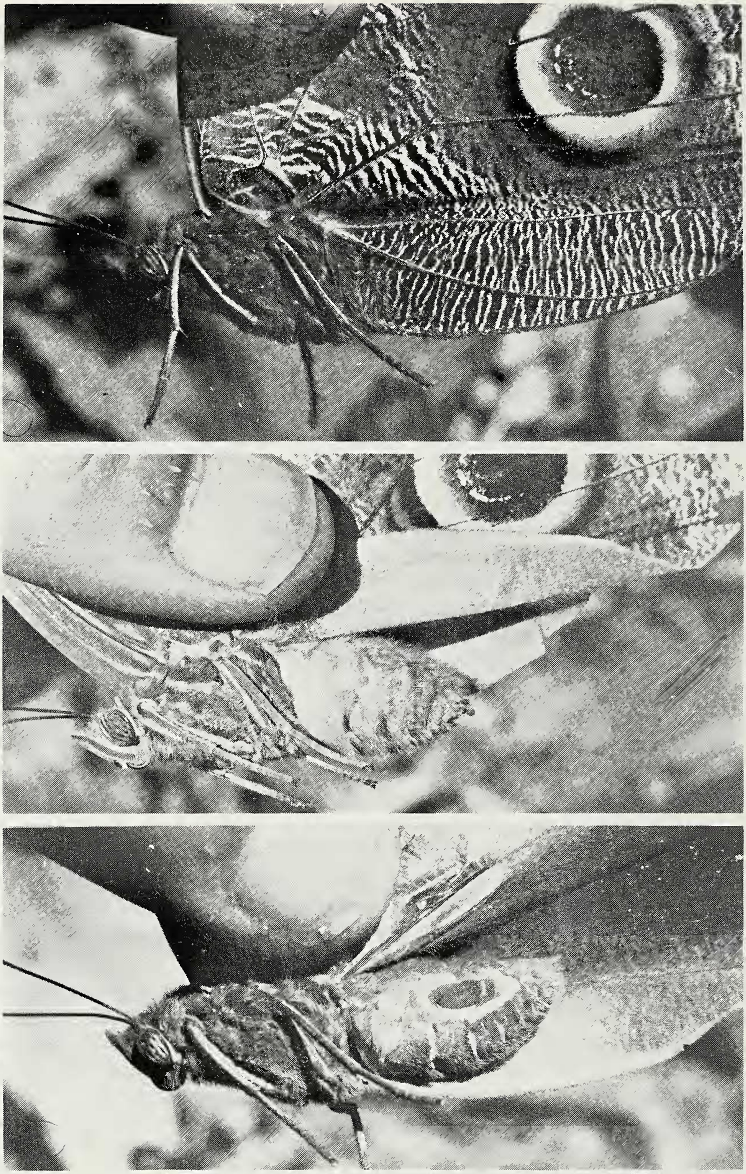

Fig. 10. Scent organ in male *C. memnon*. Top to bottom: concealment of abdominal area by hindwing in typical resting position, exposure of female abdomen, and exposure of male abdomen showing position of scent gland patches. At the Barranca Site in Costa Rica. Similar organ found in male *C. atreus*.

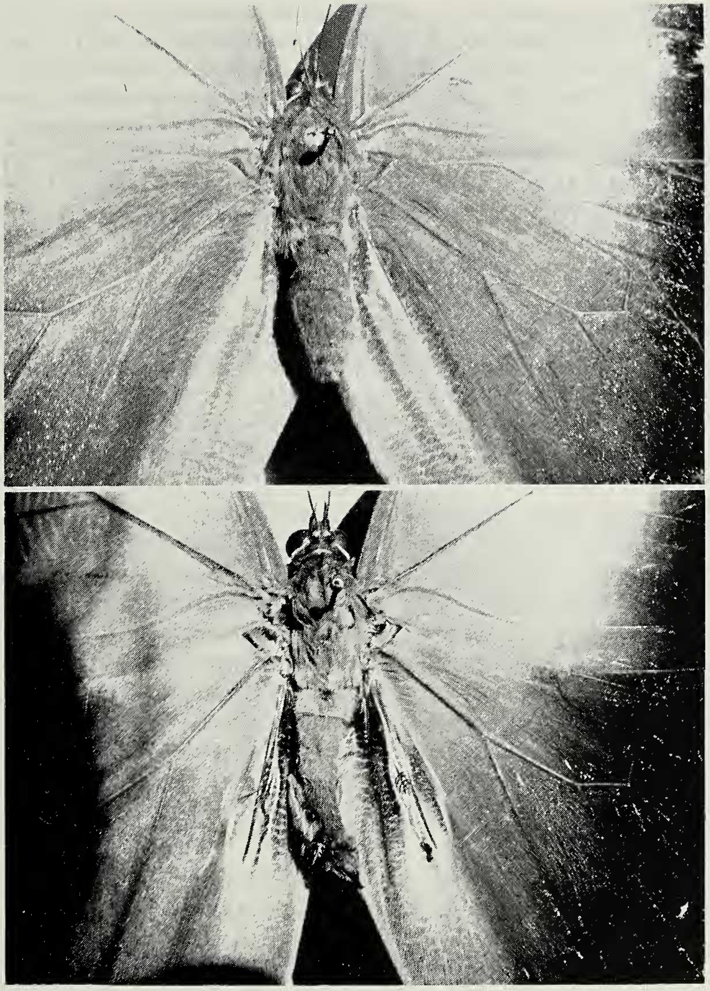

Fig. 11. Scent hairs on hindwing in male *C. memnon* (below) and absence in female (above).

Atlantic watershed. Adult population densities at experimental fruit baits on forest floors suggest that neither species is very common, but that such densities may increase facultatively during the lengthy dry season of some areas, presumably in response to moisture stress in such habitats (i.e., there being fewer moist microhabitats per unit area of habitat). In El Salvador, *C. memnon* is the common species of the genus, whereas in Costa Rica, three species in particular, *C. memnon, C. eurilochus,* and *C. atreus*, are the most familiar species in many regions. *Caligo atreus* *uranus*, the form studied in Costa Rica, represents the most northern extension of *C. atreus* from South America, having a range in Central America through Honduras (Seitz, 1924). Prior to our report, there has been no published information on the early stages and larval food plant of *C. atreus*. In this context, it is interesting to note the very marked difference in the configuration of the head capsule protuberances between this species and those of others already described (see Davis, 1915; Seitz, 1924; Harrison, 1963; Casagrande, 1979a). We suggest that the head capsule of fifth-instar *C. atreus*, as well as the prominence of silvery-gold spots on the pupa, are species-specific diagnostic characteristics that distinguish this species, including *C. memon* and *C. beltrao* (Casagrande, 1979a). Furthermore, our studies, and those of others cited in this paper, suggest that different species of *Caligo* are fairly catholic in their larval food plant associations, with most species associated with various Musaceae and Maranthaceae.

The crepuscular feeding habits of both adults and caterpillars of *Caligo*, as well as the generally cryptic appearance of these life stages, reflect a strategy of crypsis or concealment from visually-hunting diurnally-active predators. Some studies (e.g., Malo, 1961; Malo and Willis, 1961; Harrison, 1963) suggest that the early stages of *Caligo* are parasitized heavily by hymenopterans, a pattern that contributes to the generally low abundance of these butterflies in nature. Outbreak conditions of some species such as *C. eurilochus* and *C. memnon* in banana plantations in Central and South America (Harrison, 1963; Tournier, 1966) represent unusual ecological conditions favoring large increases in the population densities of herbivorous insects associated with monoculture stands of a tropical crop. In fact, the deliberate introduction of bananas into Central America from the Old World tropics may have caused a significant change in the distribution and abundance of a species such as *C. memnon*, but with little or no effect on a strictly *Heliconia* and maranthaceous-associated species such as *C. atreus*.

Acknowledgments. One of us (A.M.) was greatly assisted by his sons with various aspects of the field work in El Salvador. The Costa Rican studies are by-products of other field research projects supported by grants from the National Science Foundation (1972-1975), Friends of the Milwaukee Public Museum (1976-1977), and the American Cocoa Research Institute (1978-1983). Costa Rican larval food plants were identified with the assistance of Luis Diego Gomez and Luis Poveda of the National Museum of Costa Rica. Various students from Lawrence University assisted with the bait studies in Costa Rica (1972-1975).

Literature Cited

BARTH, R., 1954. O orgao odorifero abdominal do macho de *Caligo arisbe* Hbn. (Lepidoptera, Brassolidae). Mem. Inst. Osw. Cruz 51:203-219.

BODKIN, G. E., 1916. Report of the economic biologist. Report Dept. Sci. & Agric.

Brit. Guiana, for the 9 mos. ended 31st Dec. 1915. Georgelain, 10 pp.

BOUDAR, G., 1915. Bichos damninhos da fructicultura e arboricultura. Biblioteca Agricola Popular Brazileira, Sao Paulo, No. 22, 52 pp.

BREYER, A., 1939. Los representantes Argentinos de la familia Brassolidae. Physis. Buenos Aires 17:495-508.

BROWN, K. S., Jr., 1972. Maximizing daily butterfly counts. J. Lepid. Soc. 26:183-196.

BULLOCK, R. C., 1959. Leaf-feeding caterpillars and their control. Res. Newsletter, United Fruit Co. 6:7-15.

CASAGRANDE, M. M., 1979a. Sobre *Caligo beltrao* (Illiger). I. Taxonomia, biologia, morfologia das fases imaturas e distribuicoes espacial e temporal (Lepidoptera, Satyridae, Brassolinae). Rev. Brasil. Biol. 39:173-193.

________, 1979b. Sobre *Caligo beltrao* (Illiger). II. Morfologia externa de cabeca do adulto (Lepidoptera, Satyridae, Brassolinae). Rev. Brasil. Biol. 39:223-227.

________, 1979c. Sobre *Caligo beltrao* (Illiger). III. Morfologia externa do adulto - torax. Rev. Brasil Biol. 39:347-355.

________, 1979d. Sobre *Caligo beltrao*. IV. Morfologia externa do adulto - abdome. Rev. Brasil. Biol. 39:711-716.

CLEASE, L. D., Jr., 1926. On the life-history of *Caligo illioneus illioneus* Cram. (Lep. Morphidae). Trans. Ent. Soc. London 76:361-366.

CONDIE, S., 1976. Some notes on the biology and behavior of three species of Lepidoptera (Satyridae: Brassolinae) on non-economic plants in Costa Rica. Tebiwa 3:1-28.

CRONQUIST, A., 1968. The Evolution and Classification of Flowering Plants. Boston: Houghton-Mifflin, 396 pp.

D'ALMEIDA, R. F., 1922. Melanges Lepidopterologiques. I. Etudes sur les Lepidopteres du Bresil. Berlin: R. Friedlander & Sohn, 226 pp.

DANIELS, G. S. & F. G. STILES, 1979. The *Heliconia* taxa of Costa Rica. Keys and descriptions. Brenesia 15:1-150.

DAVIS, F. L., 1915. The larva and pupa of *Caligo memnon* Feld. Trans. Ent. Soc. London 65:198-200.

DE AZEVEDO, L. A., 1923. A praga da bananeira no Rio do Janeiro. Biologia do *Cosmopolites sordidus* Germar. Bol. Minist. Agric. Ind. & Comm. 1922, No. 5: 109-117.

DeVRIES, P. J., 1983. *Caligo memnon* (Buhito Pardo, Caligo, Cream Owl Butterfly). pp. 703-704, *In* Costa Rican Natural History (D. H. Janzen, ed.), Chicago: University of Chicago Press, 816 pp.

HARRISON, J. O., 1963. On the biology of three banana pests in Costa Rica (Lepidoptera: Limacodidae, Nymphalidae). Ann. Ent. Soc. Amer. 56:87-94.

LABRADOR, S. J. R., 1961. El genero *Opsiphanes* peligroso enemigo del cultivo del platano. Ingenieria Agron. Venez. 6:29-31.

MALO, F., 1961. Phoresy in *Xenufens* (Hymenoptera: Trichogrammatidae), a parasite of *Caligo eurilochus* (Lepidoptera: Nymphalidae). J. Econ. Ent. 54:465-466.

MALO, F. & E. R. WILLIS, 1961. Life history and biological control of *Caligo eurilochus*, a pest of banana. J. Econ. Ent. 54:530-536.

SEITZ, A., 1924. Macrolepidoptera of the World. Vol. 5: American Rhopalocera. *Caligo*: H. Fruhstorfer. Stuttgart: Kernan, 1001 pp.

STANDLEY, P. C., 1937. Flora of Costa Rica. Part I. Chicago: Field Mus. Nat. Hist. Vol. 18, Botanical Series, 398 pp.

TOURNIER, J. C., A. VILARDELO & B. SOTOMAYAR, 1966. Lepidopteres defoliateurs du bananier en Equateur: Morphologie et biologie. I. *Caligo eurilochus* Stuh. (Brassolidae). Fruits 21:57-65.

WASSERTHAL, W. & L. T. WASSERTHAL, 1980. Multinucleate neurons with neurohaemal and synapsing axons at the heart and alary muscles of the butterfly *Caligo beltrao* Illiger (Lepidoptera). Cell Tissue Res. 212:351-362.

WATERSTON, J., 1923. Notes on parasitic Hymenoptera. Bull. Ent. Res. 14:103-118.

YOUNG, A. M., 1972. Community ecology of some tropical rain forest butterflies. Amer. Midl. Nat. 87:146-157.

________, 1979. The evolution of eyespots in tropical butterflies in response to feeding on rotting fruit: an hypothesis. J. New York Ent. Soc. 87:66-77.

________, 1983. Studies on the natural history of Central American butterflies in the family cluster Satyridae-Brassolidae-Morphidae (Lepidoptera: Nymphaloidea). IV. Natural history observations on *Brassolis isthmia* in Costa Rica. J. New York Ent. Soc.: in review.

YOUNG, A. M. & A. MUYSHONDT, 1973. The biology of *Morpho peleides* in Central America. Carib. J. Sci. 13:1-49.

____________, 1975. Studies on the natural history of Central American butterflies in the family cluster Satyridae-Brassolidae-Morphidae (Lepidoptera: Nymphaloidea). III. *Opsiphanes tamarindi* and *Opsiphanes cassina* in Costa Rica and El Salvador. Studies Neotrop. Fauna 10:19-56.

Table 1. Presence of *Caligo* species on rotten banana baits* in advanced secondary and primary tropical rain forest in northeastern Costa Rica.

DATE	TIME	BUTTERFLIES PRESENT**
13 Nov. 1981	1300	none
14 Nov. 1981	1300	none
15 Nov. 1981	0830	*C. memnon* (2)
15 Nov. 1981	1400	none
4 March 1982	1200	*C. atreus* (1)
4 March 1982	1500	none
5 March 1982	0800	*C. memnon* (1); *C. atreus* (1)
5 March 1982	1200	none
5 March 1982	1500	none
5 March 1982	1700	none
6 March 1982	0800	*C. atreus* (1)
6 March 1982	1300	none
9-12 July 1982	0900	none
9-12 July 1982	1100	none
9-12 July 1982	1500	none
9-12 July 1982	1600	none
27-31 July 1982	0800	none

27-31 July 1982	1100	none
27-31 July 1982	1300	none
27-31 July 1982	1400	none
2 Dec. 1982	0645	*C. memnon* (1); *C. atreus* (1)
2 Dec. 1982	1400	none
3 Dec. 1982	0800	*C. memnon* (1)
3 Dec. 1982	1600	*C. memnon* (1)
4 Dec. 1982	0900	none
4 Dec. 1982	1000	none
4 Dec. 1982	1100	none
2 March 1983	1300	none
3 March 1983	1300	*C. memnon* (1); *C. atreus* (1)
3 March 1983	1700	*C. memnon* (2); *C. atreus* (2)
8 August 1983	0800	none
8 August 1983	1300	none
9 August 1983	0700	*C. atreus* (1)
9 August 1983	1100	none
9 August 1983	1400	*C. atreus* (1)
9-12 Nov. 1983	0800	none
9-12 Nov. 1983	1100	none
9-12 Nov. 1983	1400	none
9-12 Nov. 1983	1500	none
27-29 Feb. 1984	0900	none
3-4 Aug. 1984	1100	none
3-4 Aug. 1984	1500	none
3-4 Aug. 1984	1600	none
18 Feb. 1985	1100	none
18 Feb. 1985	1500	none
27 Feb. 1985	1200	none
27 Feb. 1985	1500	*C. memnon* (1)
28 Feb. 1985	0800	*C. memnon* (2); *C. atreus* (1)
28 Feb. 1985	0900	*C. memnon* (2)
28 Feb. 1985	1000	*C. memnon* (2); *C. atreus* (1)
28 Feb. 1985	1130	*C. memnon* (1)
28 Feb. 1985	1400	none
3 March 1985	0800	none
3 March 1985	1000	none
3 March 1984	1200	none
3 March 1985	1330	none
3 March 1985	1500	none

*Two piles of vinegary-smelling, rotten bananas, each approximately 0.5 m diameter and roughly 40 m apart, were placed on the ground in the same places for all censuses. Baits were distributed the day before butterfly observations began.

**Data here excludes sightings of other butterflies (e.g., *Morpho*). Figures in parentheses refer to numbers of individuals seen.